Historical Biology 2018

Unusual archosaur trackway and associated tetrapod ichnofauna from Irohalene member (Timezgadiouine formation, late Triassic, Carnian) of the Argana Basin, Western High Atlas, Morocco

Kazan Federal University, 420008, Kremlevskaya 18, Kazan, Russia

Abstract

© 2018, © 2018 Informa UK Limited, trading as Taylor & Francis Group. An archosaur trackway consisting of 10 successive pes imprints has been recovered from the Late Triassic Irohalene Member of the Timezgadiouine Formation (Argana Basin, Morocco). Footprints are tetradactyl-pentadactyl, and show an elongated 'heel', probably enclosing the trace of digit V. The trackway lacks a manus impression, which could be due to bipedal progression of the trackmaker or be a preservational phenomenon. It is assigned to cf. Parachirotherium isp. based on similarities with the ichnogenus that has been described from the same stratigraphic unit. Other footprints of this assemblage are assigned to the ichnotaxa Grallator-Eubrontes (dinosauromorphs/crocodilian-stem archosaurs), Brachychirotherium isp. (crocodilian-stem archosaurs), Rhynchosauroides isp. (lepidosauromorphs/archosauromorphs), and indeterminate ichnotaxa. Associated with the footprints are numerous invertebrate traces such as Scoyenia gracilis. The ichnofauna of the Irohalene Member supports a cosmopolitan distribution of pentadactyl but functionally tridactyl chirotheres (Parachirotherium) and grallatorids across the Ladinian-Carnian boundary. Similar assemblages are known from the Germanic Basin and from Eastern North America. Furthermore, it documents the occurrence of very large Eubrontes trackmakers in the early Carnian. The depositional environment of the lower part of the Irohalene Member is interpreted as wet red beds of a flood basin transitional to a distal braid plain.

http://dx.doi.org/10.1080/08912963.2018.1513506

Keywords

Archosaurs, Carnian, Irohalene Member, Morocco, Scoyenia ichnofacies, Tetrapod footprints

References

[1] Avanzini M, Petti FM, Bernardi M, Tomasoni R., 2010. Crocodile-like footprints from the Upper Triassic (Carnian) of the Italian Southern Alps. Crocodyle Tracks and Traces. New Mexico Mus Nat His Sci Bull. 51:61–64

[2] Avanzini M, Renesto S. 2002. A review of Rhynchosauroides tirolicus Abel, 1926 ichnospecies (Middle Triassic: anisian-Ladinian) and some inferences on Rhynchosauroides trackmaker. Rivista Italiana Di Paleontologia Stratigrafia. 108(1):51–66

[3] Baird D. 1957. Triassic reptile footprint faunules from Milford, New Jersey. Bull Museum Comp Zool. 117:449–520

[4] Biron PE, Dutuit J-M. 1981. Figurations sédimentaires et traces d'activité au sol dans le Trias de la formation d'Argana et de l'Ourika (Maroc). Bulletin Du Muséum National d'Histoire Naturelle 4e, 3rd Series, Section C, N. 4:399–427

[5] Brown RH. 1980. Triassic rocks of Argana Valley, Southern Morocco and their regional structural implications. Bull Am Assoc Petroleum Geol. 64:988–1003

[6] D'Orazi-Porchetti S, Nicosia U, Mietto P, Petti FM, Avanzini M. 2008. Atreipus-like footprints and their co-occurrence with Evazoum from the upper Carnian (Tuvalian) of Trentino-Alto Adige. Studi Trentini di Scienze Naturali Acta Geologica. 83:277–287

[7] Desojo JB, Heckert AB, Martz JW, Parker WG, Schoch RR, Small BJ, Sulej T. 2013. Aetosauria: a clade of armoured pseudosuchians from the Upper Triassic continental beds. Geo Soc, London, Special Publications. 379(1):203–239

[8] Dutuit JM., 1976. Introduction à l'étude paléontologique du Trias continental marocain. Description des premiers Stégocephales recueillis dans le couloir d'Argana (Atlas occidental). Mémoires du Muséum National d'Histoire naturelle, Paris, Séries C 36, 1–253

[9] Dutuit JM. 1977a. Paleorhinus magnoculus, Phytosaure du Trias supérieur de l'Atlas marocain. Annales Université Provence Géologie Méditerranéenne. 4(3):255–267

[10] Dutuit JM. 1977b. Description du crâne de Angistorhinus talainti n. sp. un nouveau phytosaure du Trias atlasique marocain. Bulletin Muséum National Histoire Naturelle, Paris, Séries 3. 489:297–324

[11] El Arabi EH, Diez JB, Broutin J, Essamoud R. 2006. Première caractérisation palynologique du Trias moyen dans le Haut Atlas; implications pour l'initiation du rifting téthysien au Maroc. C R Geosci. 338(9):641–649

[12] Farlow JO, Schachner ER, Sarrazin JC, Klein HK, Currie PJ. 2014. Pedal proportions of Poposaurus gracilis: convergence and divergence in the feet of archosaurs. Anatomical Rec. 297:1022–1046

[13] Flynn JJ, Nesbitt SJ, Parrish JM, Ranivoharimanana L, Wyss AR. 2010. A new species of Azendohsaurus (Diapsida: archosauromorpha) from the Triassic Isalo Group of southwestern Madagascar: cranium and mandible. Palaeontology. 53(3):669–688

[14] Gierliński G, Ahlberg A. 1994. Late Triassic and Early Jurassic dinosaur footprints in the Höganäs formation of southern Sweden. Ichnos. 3(2):99–105

[15] Harding AG, Brown RH. 1974. Structural controls over thickness and facies distributions in a Late Triassic–early Jurassic carbonate–sulfate-redbed sequence in southwestern Morocco, and its relationship to the opening of the Atlantic. Geol Soc America, Abstr with Programs. 7:1099–1100

[16] Haubold H. 1971. Ichnia Amphibiorum et Reptiliorum fossilium. Encyclopedia of Paleoherpetology. 18:1–124

[17] Haubold H, Klein H. 2000. Die dinosauroiden Fährten Parachirotherium–atreipus–grallator aus dem unteren Mittelkeuper (Obere Trias: ladin, Karn, ?Nor) in Franken. Hallesches Jahrbuch für Geowissenschaften B. 22:59–85

[18] Haubold H, Klein H. 2002. Chirotherien und Grallatoriden aus der Unteren bis Oberen Trias Mitteleuropas und die Entstehung der Dinosauria. Hallesches Jahrbuch für Geowissenschaften B. 24:1–22

[19] Heckert AB, Lucas SG, Rinehart LF, Celeskey MD, Spielmann JA, Hunt AP. 2010. Articulated skeletons of the aetosaur Typothorax coccinarum Cope (Archosauria: stagonolepididae) from the Upper Triassic Bull Canyon Formation (Revueltian: early-Mid Norian), Eastern New Mexico, USA. J Vert Paleontol. 30(3):619–642

[20] Hitchcock E., 1858. Ichnology of New England. A Report on the Sandstone of the Connecticut Valley, Especially its Fossil Footmarks, Made to the Government of the Commonwealth of Massachusetts. William White, Printer. Boston, 1-214

[21] Hmich D, Schneider JW, Saber H, Voigt S, El Wartiti M. 2006. New continental Carboniferous and Permian faunas of Morocco: implications for biostratigraphy, palaeobiogeography and palaeoclimate. Geol Soc London, Special Publications. 265:297–324

[22] Hminna A. 2013. La limite Permien supérieur - Trias du Bassin d'Argana (Haut-Atlas) et le Trias supérieur du Bassin de sidi Said Maachou (Meseta Occidentale) (Maroc); Biostratigraphie, Sédimentologie, Tectonique et Géochimie. El Jadida (Maroc): Thèse de doctorat de l'Université Chouaïb Doukkali, Faculté des Sciences; p. 255

[23] Hminna A, Voigt S, Klein H, Saber H, Schneider JW, Hmich D. 2013. First occurrence of tetrapod footprints from the continental Triassic of the Sidi Said Maachou area (Western Meseta, Morocco). J Afr Earth Sci. 80:1–7

[24] Hminna A, Voigt S, Saber H, Schneider JW, 2008. On a diverse continental ichnofauna of the Permian Ikakern formation (Argana Basin, Western High Atlas, Morocco). Ichnia, Second International Congress on Ichnology, Aug29 - 2008 Sept8, Cracow (Poland), Abstract Book:52–53

[25] Hminna A, Voigt S, Saber H, Schneider JW, Hmich D, 2009. Tetrapod footprints from the Ikakern Formation (Argana Basin, Western High Atlas, Morocco). Abstract volume, First International Congress on North African Vertebrate Palaeontology, Marrakech, May 25–27:61–62

[26] Hminna A, Voigt S, Saber H, Schneider JW, Hmich D. 2012. On a moderately diverse continental ichnofauna from the Permian Ikakern formation (Argana Basin, Western High Atlas, Morocco). J Afr Earth Sci. 68:15–32

[27] Hminna A, Zouheir T, Klein H, El Maliki S, Lagnaoui A, Saber H, Schneider JW, 2017. Large archosaur footprints from the late Triassic of Irohalene (Argana Basin, Western High Atlas, Morocco).The First International ASRO Geological Congress, El Jadida (Morocco), 2017 Mar15–17. Abstracts. 45 pp

[28] Hofmann A, Tourani A, Gaupp R. 2000. Cyclicity of Triassic to Lower Jurassic continental red beds of the Argana Valley, Morocco: imlications for palaeoclimate and basin evolution. Palaeogeogr Palaeoclimatol Palaeoecol. 161:229–266

[29] Hunt AP, Lucas SG. 2007. Tetrapod ichnofacies: a new paradigm. Ichnos. 14(1–2):59–68

[30] Jalil NE. 1999. Continental Permian and Triassic vertebrate localities from Algeria and Morocco and their stratigraphical correlations. Journal of African Earth Sciences. 29(1):219-226

[31] Jalil NE, Janvier P, Steyer JS. 2009. A new cyclotosaurid (Amphibia,Temnospondyli) from the Triassic of Argana Basin (High Atlas Mountains, Morocco); biostratigraphic implications: first International Congress on North African Vertebrate PalaeontologyAbstract Volume. 36–37

[32] Jalil NE, Peyer K. 2007. A new rauisuchian (Archosauria, Suchia) from the Upper Triassic of the Argana Basin, Morocco. Palaeontology. 50(2):417–430

[33] Jones DF, 1975. Stratigraphy, environments of deposition, petrology, age and provenance of the basal red beds of the Argana Valley, western High Atlas Mountains, Morocco. Unpublished MSc thesis, New Mexico Institute of Mining and Technology, Socorro. 148 pp

[34] Kammerer CF, Nesbitt SJ, Shubin NH. 2011. The first basal dinosauriform (Silesauridae) from the Late Triassic of Morocco. Acta Palaeontol Pol. 57(2):277–284

[35] Karl C, Haubold H. 1998. Brachychirotherium aus dem Coburger Sandstein (Mittlerer Keuper, Karn/Nor) in Nordbayern. Hallesches Jahrbuch Für Geowissenschaften B. 20:33–58

[36] Karl C, Haubold H. 2000. Saurierfährten im Keuper (Obere Trias) Frankens, die Typen von Brachychirotherium. Berichte Der Naturwissenschaftlichen Gesellschaft Bayreuth. 24:91–120

[37] Klein H, Lucas SG, Haubold H. 2006. Tetrapod track assemblage of the Redonda Formation (Upper Triassic, Chinle Group) in east-central New Mexico–re-evaluation of ichnofaunal diversity from studies of new material. In: Jd H, Sg L, Ja S, Lockley MG, Arc M, Ji K, editors. The Triassic-Jurassic Terrestrial Transition, Vol. 37. New Mexico Museum of Natural History and Science, Bulletin; p. 241–250.London: Special Publication

[38] Klein H, Haubold H. 2007. Archosaur footprints-potential for biochronology of Triassic continental sequences. New Mexico Museum Of Natural History and Science Bulletin. 41:120-130

[39] Klein H, Kneidl V. 2015. Tetrapodenfährten aus den Estherienschichten (Obertrias, Grabfeld-Formation) der Tongrube Barbaraberg (Speinshart, NO-Bayern)–profilaufnahme, Bildungsmilieu und Hinweise zur Palökologie. Geologische Blätter Für Nordost-Bayern. 65(2–4):93–130

[40] Klein H, Lucas SG. 2010. Tetrapod footprints - their use in biostratigraphy and biochronology of the Triassic. Geological Society, London, Special Publications. 334:419-446

[41] Klein H, Milán J, Clemmensen LB, Frobøse N, Mateus O, Klein N, Adolfssen JS, Estrup EJ, Wings O. 2016. Archosaur footprints (cf. Brachychirotherium) with unusual morphology from the Upper Triassic fleming Fjord formation (Norian–rhaetian) of East Greenland. Geol Soc. 434:71–85. (London, Special Publication)

[42] Klein H, Niedźwiedzki G, Voigt S, Lagnaoui A, Hminna A, Saber H, Schneider JW. 2013. The tetrapod ichnogenus Protochirotherium Fichter and Kunz 2004, a characteristic Early Triassic morphotype of central pangea. Ichnos. 20:24–30

[43] Klein H, Saber H, Voigt S, Schneider JW, Hmich D, Hminna A. 2009. An archosaur-dominated footprint assemblage in Permo-Triassic red-beds of Morocco and the global record of early chirotherians. In: Abstracts. First International congress on North African vertebrate palaeontology. p. 18

[44] Klein H, Voigt S, Hminna A, Saber H, Schneider J, Hmich D. 2010. Early Triassic Archosaur-dominated footprint assemblage from the Argana Basin (Western High Atlas, Morocco). Ichnos. 17:215–227

[45] Klein H, Voigt S, Saber H, Schneider JW, Hminna A, Fischer J, Lagnaoui A, Brosig A. 2011. First occurrence of a Middle Triassic tetrapod Ichnofauna from the Argana Basin (Western High Atlas, Morocco). Palaeogeogr Palaeoclimatol Palaeoecol. 307:218–231

[46] Kuhn O. 1958. Die Fährten der vorzeitlichen Amphibien und Reptilien. Bamberg: Meisenbach; p. 64

[47] Lagnaoui A, 2014a. Late Paleozoic and Early Mesozoic continental ichnofaunas of Morocco (Sidi Kassem, Souss, Tiddas and Argana basins): Ichnotaxonomy, Paleoecology and Biostratigraphy. Upublished PhD thesis, Faculty of Sciences, Chouaïb Doukkali University, Morocco. 215 pp

[48] Lagnaoui A. 2014b. Late Palaeozoic and Early Mesozoic Continental Ichnofossils from Morocco: biostratigraphy, Palaeoecology end end-Permian Biotic Crisis evidence. Arabian J Earth Sci. 1(4):26–35

[49] Lagnaoui A, Klein H, Saber H, Fekkak A, Belahmira A, Schneider JW. 2016. New discoveries of archosaur and other tetrapod footprints from the Timezgadiouine Formation (Irohalene Member, Upper Triassic) of the Argana Basin, western High Atlas, Morocco–ichnotaxonomic implications. Palaeogeogr Palaeoclimatol Palaeoecol. 453:1–9

[50] Lagnaoui A, Klein H, Voigt S, Hminna A, Saber H, Schneider JW, Werneburg R. 2012. Late Triassic tetrapod-dominated ichnoassemblages from the Argana Basin (Western High Atlas, Morocco). Ichnos. 19:238–253

[51] Lagnaoui A, Klein H, Voigt S, Hminna A, Saber H, Schneider JW, Werneburg R, 2013a. The Permian-Triassic tetrapod ichnofaunal diversity of continental red-beds in Morocco: their Biostratigraphic and Paleoecologic potentials. 24th Colloquium of African Geology (CAG24), Geological Society of Africa (GSAf), January 8–14, Millennium Hall, Addis Abeba (Ethiopia). 101

[52] Lagnaoui A, Klein H, Voigt S, Hminna A, Saber H, Schneider JW, Werneburg R, 2013b. Tetrapod Footprint ichnofauna of the late Triassic Timezgadiouine and Bigoudine formations of the Argana Basin (Western High Atlas, Morocco). 24th Colloquium of African Geology (CAG24), Geological Society of Africa (GSAf), 2013 Jan8–14, Millennium Hall, Addis Abeba (Ethiopia). 100 pp

[53] Leonardi G, ed. 1987. Glossary and manual of tetrapod footprint palaeoichnology. Brasilia: Ministerio Minas Energie, Departemento Nacional Producao Mineral; p. 117

[54] Lockley MG, Hunt AP. 1995. Ceratopsid tracks and associated ichnofauna from the Laramie formation (Upper Cretaceous: maastrichtian) of Colorado. J Vert Paleontol. 15(3):592–614

[55] Lucas SG. 2010. The Triassic timescale based on nonmarine tetrapod biostratigraphy and biochronology. In: Sg L, editor. The Triassic timescale, Vol. 334. Geological Society of London Special Publication; p. 447–500

[56] Lucas SG. 2018. Late Triassic terrestrial tetrapods: biostratigraphy, biochronology and biotic events. In: Tanner LH, editor. The late Triassic World, topics in geobiology. Springer International Publishing, 46. doi:10.1007/978-3-319-68009-5_10

[57] Lucas SG, Heckert AB. 2011. Late Triassic Aetosaurs as the Trackmaker of the Tetrapod Footprint Ichnotaxon Brachychirotherium: Ichnos. 18(4):197–208

[58] Lucas SG, Klein H, Lockley MG, Spielmann J, Gierlinski GD, Hunt AP, Tanner LH. 2006. Triassic-Jurassic stratigraphic distribution of the theropod footprint ichnogenus Eubrontes. New Mexico Museum of natural history and science. Bulletin. 37:68–93

[59] Lucas SG, Spielmann JA, Klein H, And Lerner AJ. 2010. Ichnology of the upper Triassic Redonda formation (Apachean) in east-central New Mexico. New Mexico Museum of Natural History and Science, Bulletin. 47:75

[60] Maidwell FT. 1911. Notes on footprints from the Keuper of Runcorn hill. Proc Liverpool Geol Soc. 11(2):140–152

[61] Marchetti L, Voigt S, Klein H. 2017. Revision of Late Permian tetrapod tracks from the Dolomites (Trentino-Alto Adige, Italy). Hist Biol. 1–36. doi:10.1080/08912963.2017.1391806

[62] Medina F, Tourani A, Benaouiss N, Jalil NE. 2000. Les Bassins d'Argana. AGP-GMPT 486. Field Guide 'Permian Basins of Morocco'; p. 17

[63] Medina F, Vachard D, Jp C, Ouarhache D, Ahmamou M. 2001. Charophytes et ostracodes du niveau carbonaté de Taourirt Imzilen (Membre d'Aglegal, Trias d'Argana); implications stratigraphiques. Bulletin De L' Institut Scientifique. 23:21–26

[64] Niedźwiedzki G. 2011. A late Triassic dinosaur-dominated ichnofauna from the Tomanová Formation of the Tatra Mountains, Central Europe. Acta Palaeontol Pol. 56(2):291–300

[65] Olsen PE., Et-Touhami M., 2008. Tropical to subtropical syntectonic sedimentation in the Permian to Jurassic Fundy Rift Basin, Atlantic Canada, in relation to the Moroccan conjugate margin: in Brown, D.E. (ed.), Central Atlantic Conjugate Margins, Program and Extended Abstract: Dalhousie University Halifax, Nova Scotia, 121 p

[66] Olsen PE, Huber P. 1998. The oldest late Triassic footprint assemblage from North America (Pekin Formation, Deep River Basin, North Carolina, USA). Southeast Geol. 38:77–90

[67] Olsen PE, Smith JB, McDonald NG. 1998. Type material of the type species of the classic theropod footprint genera Eubrontes, Anchisauripus, and Grallator (Early Jurassic, Hartford and Deerfield basins, Connecticut and Massachusetts, USA). J Vert Paleontol. 18(3):586–601

[68] Saber H, 1998. The Stephano-Permian of the western High Atlas: geological and geodynamic evolution (Morocco). Doctorat Es-Sciences (thèse d'Etat), Chouaïb Doukkali University, El Jadida (Morocco), 212 pp

[69] Saber H, El Wartiti M, Broutin J. 2001. Dynamic sedimentology of two Upper Stephano-Lower Permian basins: ida Ou Zal and Ida Ou Ziki, western High Atlas, Morocco. J Afr Earth Sci. 32:573–594

[70] Saber H, El Wartiti M, Hmich D, Schneider JW. 2007. Tectonic evolution from the Hercynian shortening to the Triassic extension in the Paleozoic Western High Atlas (Morocco). J Iberian Geol. 33(1):31–40

[71] Schneider JW, Lucas SG, Werneburg R, Röβler R. 2010. Euramerican late Pennsylvanian/Early Permian arthropleurid/tetrapod associations–implications for the habitat and paleobiology of the largest terrestrial arthropod. In: Lucas SG, Schneider JW, Ja S, editors. Carboniferous-Permian transition in Canon del Cobre, northern New Mexico, Vol. 49. New Mexico Museum of Natural History and Science, Bulletin; p. 49–70

[72] Sereno PC. 1991. Basal archosaurs: phylogenetic relationships and functional implications. J Vert Paleontol. 11(S4):1–53

[73] Smith JB, Farlow JO. 2003. Osteometric approaches to trackmaker assignment for the Newark Supergroup ichnogenera Grallator, Anchisauripus, and Eubrontes. In: Pm L, Pe O, editors. The great rift valleys of Pangea in Eastern North America, Volume 2. Sedimentology, stratigraphy and paleontology. New York: Columbia University Press; p. 273–292

[74] Tixeront M. 1973. Lithostratigraphie et minéralisation cuprifères et uranifères stratiformes syngénétiques et familières des formations détritiques permo-triasiques du Couloir d'Argana (Haut-Atlas occidental, Maroc). Notes Mémoires Du Service Géologique Du Maroc. 33(249):147–177

[75] Tixeront M. 1974. Carte géologique et minéralogique du Couloir d'Argana, 1/100 000. Edition du Service Géologique du Maroc, Notes et Mémoires; p. 205

[76] Voigt S, Hminna A, Saber H, Schneider JW, Klein H. 2010. Tetrapod footprints from the uppermost level of the Permian Ikakern Formation (Argana Basin, Western High Atlas, Morocco). J Afr Earth Sci. 57:470–478

[77] Voigt S, Schneider JW, Saber H, Hminna A, Lagnaoui A, Klein H, Brosig A, Fischer J. 2011. Complex tetrapod burrows from middle Triassic red beds of the Argana Basin (Western High Atlas, Morocco). Palaios. 26(9):555–566

[78] Weems RE. 2003. Plateosaurus foot structure suggests a single trackmaker for Eubrontes and Gigandipus footprints. In: Pm L, Pe O, editors. The great rift valleys of Pangea in eastern North America. New York: Columbia University Press; p. 293–313

[79] Zouheir T, Hminna A, Klein H, Lagnaoui A, Saber H, Schneider JW. 2018. Tetrapod footprints from the late Triassic of Irohalene (Argana Basin, Western High Atlas, Morocco) - most recent update and paleoenvironmental implications. Second International Congress on Permian and Triassic; April 25–27; Casablanca (Morocco); p. 55–56